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Studies on southern Australian abalone (genus *Haliotis*) XVIII. Ring formation in *H. scalaris*

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Abstract

The abalone *Haliotis scalaris* deposits two fine rings a year in the spire, one in about December and the other from May to July, corresponding roughly to summer and winter sea temperature extremes. Additional fine rings, and in particular brown rings, are deposited in response to boring annelids and drilling muricid gastropods. Multiple regression analysis revealed a relationship between the number of rings in the spire and the variables: age of the shell, extent of infestation by annelids, and the number of brown rings. The analysis showed that additional fine rings and brown rings are deposited according to the degree of parasitic attack.

Keywords: *Haliotis scalaris*; rings; shell aging; parasite attack; endobionts; muricid drilling.

Introduction

The use of shell rings to age the shells of abalone is now an established technique although nearly every species so far studied appears to have unique features (Shepherd *et al.* 1995; Shepherd and Avalos-Borja 1997). In *Haliotis fulgens* and *H. corrugata*, pigmented and non-pigmented rings were observed and an understanding of the pattern of deposition of each was necessary for correct interpretation (Shepherd and Turrubiates-Morales 1997; Shepherd and Avalos-Borja 1997).

Haliotis scalaris Leach is a small, non-commercial abalone which lays down pigmented and non-pigmented rings (called brown and fine rings respectively) of prismatic structure in the spire. As the growth rate of this species is well known from earlier studies (Shepherd *et al.*1988) we examined the pattern of deposition of rings in relation to growth and intensity of infestation of the shell by parasites, in order to evaluate the use of rings to age the shell. Earlier studies (Shepherd 1973 and see review of Shepherd and Breen 1992) have shown that the main parasites of this abalone at West Island are annelids, especially *Polydora* spp., which are endobionts in the shell, and muricid gastropods (mainly *Haustrum baileyanum*) which drill holes in the shell through which they feed (Thomas and Day 1995).

Materials and methods

Monthly samples of 10–15 shells (142 in all) of *H. scalaris* in the size range 19–88 mm shell length(SL) were taken at West Island, South Australia (35°37'S; 138°35'E), from November 1993 to February 1995. The spires of the shells were ground horizontally with an electric sander until a minute hole appeared, polished with 200–600 grit fine emery paper (see Shepherd *et al.* 1995), and then etched with dilute HCl. The shell length was measured and the number of fine (i.e. non-pigmented) and brown (i.e. pigmented) rings counted. Unreadable shells (see below) were discarded.

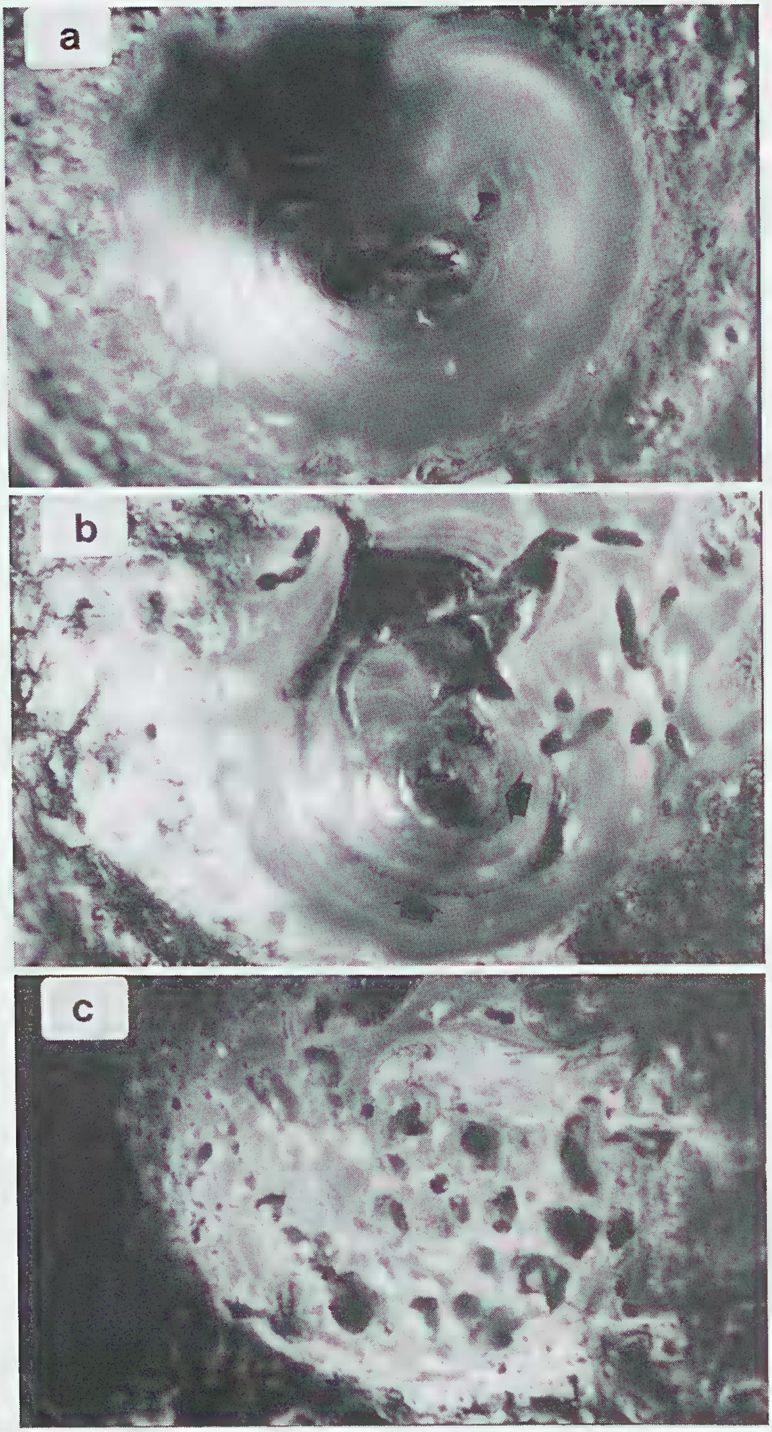

Figure 1. **a** – Photograph of horizontal section in the spire of *H. scalaris* (infestation score 0) showing 12 fine rings; **b** – Horizontal section in the spire of *H. scalaris* (infestation score 1) showing (arrowheads) brown rings; **c** – Horizontal section in the spire of *H. scalaris* (infestation score 3) which is unreadable.

The extent of infestation of each shell by annelid parasites in the region of the spire was estimated on an infestation scale ranging from 0 (no parasites) to 3 (heavily infested and often unreadable) and the number of muricid bore-holes counted.

Results

The spires of shells, uninfested, slightly infested and with brown rings, and heavily infested, are shown in Fig. 1. Brown rings are conspicuous because they are impregnated with pigmented conchiolin-like material, but often the polishing process leaves deep excavations in the section where the conchiolin deposits have been removed (Fig. 1 b).

The incidence of infestation is low in shells < ~50 mm SL but then increases sharply with shell size so that nearly all shells > 75 mm SL are heavily infested and unreadable (Fig. 2). In addition 9% of the shells in the range 57–75 mm SL had been drilled once or more times by muricids, probably *Haustrum baileyanum*, which is common in the vicinity. A plot of the total number of fine and brown rings vs shell length, in which we distinguish shells according to degree of infestation and presence of brown rings (Fig. 2), shows a clear tendency for seriously infested shells with brown rings to have more fine rings for a given length than shells with light or no infestation. As the growth rate of *H. scalaris* is linear with length over the length range examined (Shepherd *et al.*

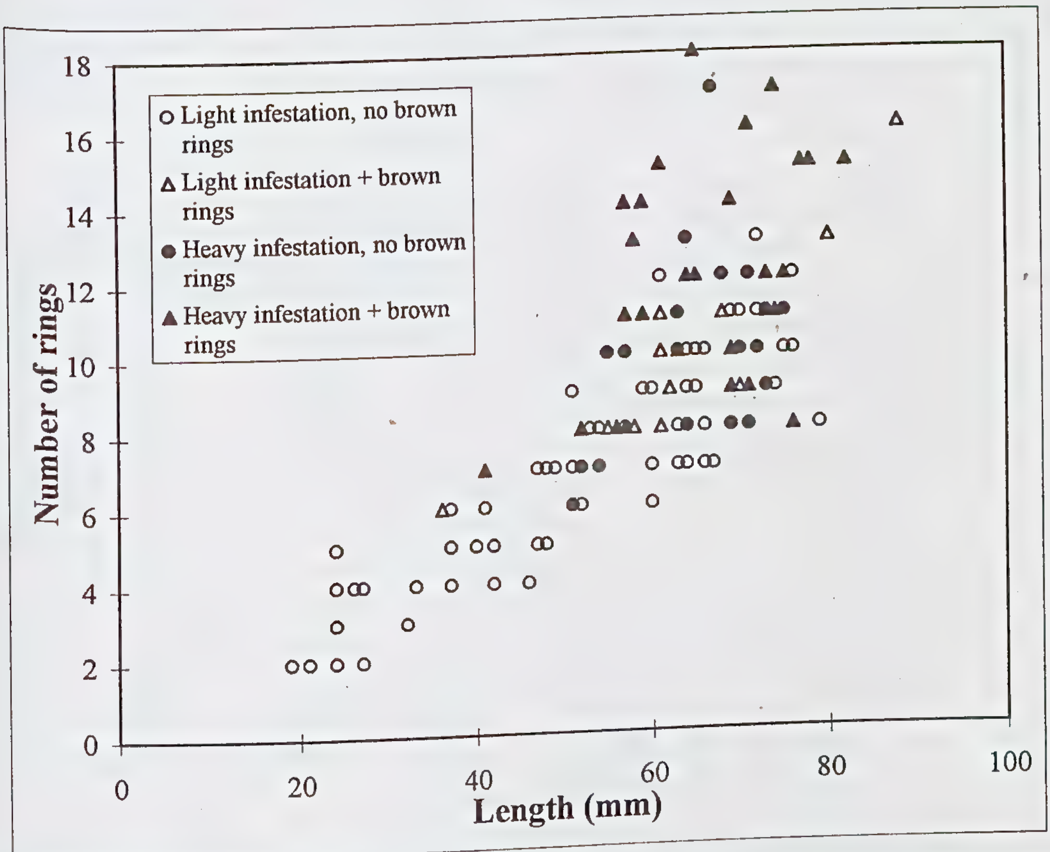

Figure 2. Plot of total number of rings vs shell length of shells of *H. scalaris* for lightly infested shells (infestation score 0 and 1) and more severely infested shells (infestation score 2 and 3) with and without brown rings.

1988), length is a good estimator of age, so shell length (SL) in mm was converted to age (A) in years by the relation:

$$SL = 0.008 + 13.61\ A$$

This equation indicates a mean growth rate of 13.6 mm a year (Shepherd *et al.* 1988). A regression of the number of rings (R) vs age of the subset of shells with an infestation score of zero and without brown rings gave the regression equation:

$$R = -0.53 + 1.96\ A\ (R^2=0.77;\ N=59)$$

The standard error of the slope was 0.13 indicating that the slope did not differ significantly from the integer 2. So we concluded that 2 fine rings a year were laid down in these shells.

Effect of infestation and muricid bore-holes

Of the 11 shells with bore-holes in them, there was a significant correlation between the number of brown rings and the number of bore-holes ($r=0.63$; $P<0.05$). Two of these shells had bore-holes but no brown rings. In addition, there were 29 other shells with brown rings and a mean infestation score of 2.0 (s.e.0.1) but no detectable bore-holes. A multiple linear regression analysis of the total number of fine *and* brown rings (R) vs age (A), the number of brown rings (BR), and the infestation score (I), after excluding unreadable shells, gave the regression equation (standard errors in brackets):

$$R = -0.56(0.71) + 1.93(0.17)\ A + 1.05(0.22)\ BR + 0.48(0.22)I\ (R^2=0.70;\ N=118)$$

The constant did not differ significantly from zero ($t=0.8$; ns), but the other coefficients were significant (for A, $t=11.4$, $P<0.0001$; for BR $t=4.8$, $P<0.0001$; for I $t=2.2$, $P<0.05$). Thus, for all readable shells age accounted for 2 rings a year, boring of the shell for 0.5 rings per unit infestation score, and brown rings for one ring. This last constant means that brown rings are themselves adventitious and do not cause the deposition of extra rings.

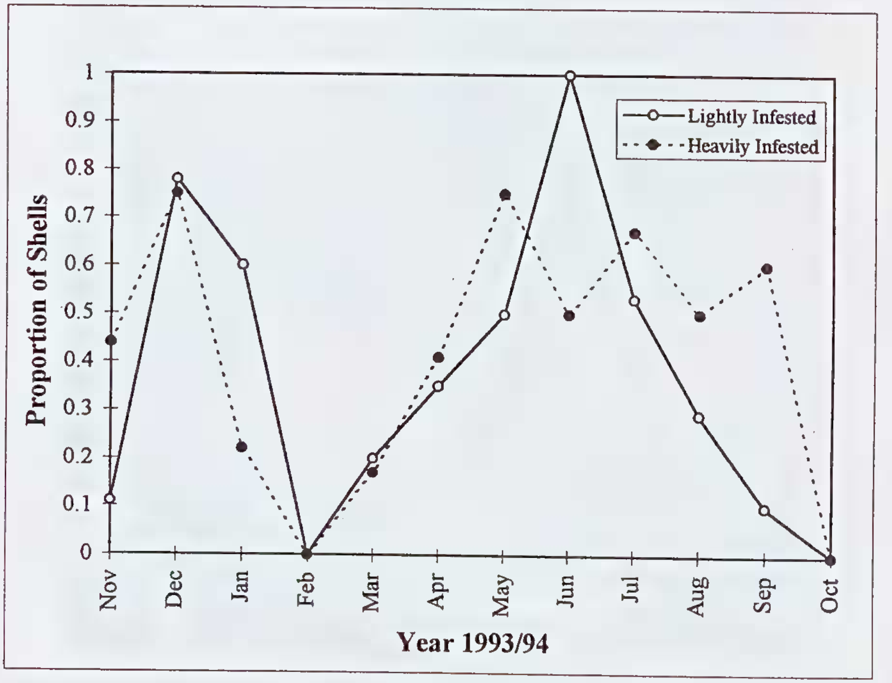

Figure 3. Monthly distribution of proportion of shells of *H. scalaris* with a recently deposited ring in lightly infested shells (infestation score 0 and 1) shown in open circles,and more seriously infested shells (infestation score 2 and 3) shown in closed circles.

Timing of ring deposition

When viewed in horizontal section prismatic rings are opaque whereas layers of aragonite are translucent. Thus, examination of the interior surface of the shell near the spire in monthly samples indicates the approximate months in which rings were deposited. This was confirmed where possible by examination of the innermost ring in the horizontal section at the spire. A plot of the percentage frequency of recently deposited rings by month for (a) shells with infestation scores of 0 or 1, and (b) shells with infestation scores of 2 or 3 (Fig. 3) shows that ring deposition is concentrated in the May to July period and December in the slightly infested group of shells but more diffusely around the same seasonal peaks in the more seriously infested group of shells.

Discussion

The pattern of deposition of rings in *H. scalaris* differs from that of other abalone species which lay down one ring a year (Prince *et al*. 1988; Erasmus *et al*. 1994; Shepherd and Avalos-Borja 1997) or a variable number of rings (Shepherd and Turrubiates 1997). In *H. scalaris* ring deposition occurs as sea temperatures approach their respective maxima and minima (see Shepherd and Womersley 1970). Possibly sea temperature is the exogenous factor controlling ring deposition in this species (reviewed by Tevesz and Carter 1980 for bivalve molluscs) although seasonal variation in day length would equally well explain our data.

Infested shells clearly have more fine rings for a given size than uninfested shells (Fig. 2). There are two possible causes of this. One is that infested shells grow more slowly as the infested abalone devotes relatively more energy to shell repair than to growth (Shepherd and Breen 1992). Hence infested shells would be smaller for a given age than uninfested shells and so would appear to have deposited more than two rings a year. Alternatively, extra fine rings may be deposited in response to infestation. Gabriel (1981) found that calcite was more resistant to borers than aragonite, so deposition of prismatic layers would be adaptive. Our data are consistent with both hypotheses, but the large number of extra fine rings laid down in infested shells suggest that the latter effect (extra rings) is the greater of the two. Shepherd and Triantafillos (1997) also concluded that polydorid boring induced extra rings to be deposited in *H. laevigata*. The correlation between the number of muricid bore-holes and the number of brown rings and the multiple regression analysis together support the hypothesis that drilling by muricid snails causes the deposition of brown rings. Thomas and Day (1995) found that artificial holes which mimicked the drilling of muricids caused *H. rubra* to secrete a black proteinaceous deposit around the holes, and our own observations on many shells of *H. scalaris* confirm that brown deposits around bore-holes is a common response to drilling by *H. baileyanum*. However, the occurrence of brown layers (or rings) in the spire of infested shells without bore-holes suggests that deposition of brown rings is a general response to irritation by parasites or endobionts of the shell, and that the brown ring is not restricted to the precise location of the parasite's attack.

The relation between the brown rings observed by us in *H. scalaris* and *H. laevigata* (Shepherd and Triantafillos 1997) and the brown ring disease widely reported in bivalves (Paillard *et al.* 1994; Perkins 1996) is unclear. Both are characterised by brown conchiolin deposits on the inner surface of the shell and are associated with irritation of the mantle by parasites and commensals. However, in the case of the brown ring disease the causative agent is a species of *Vibrio* which can lead to high mortalities, whereas in abalone there is no evidence that the brown rings are pathological.

How useful are rings for aging *H. scalaris* given the several apparent causes of ring deposition? Discarding a large proportion of a sample because of shell infestation, as Nash (1992) found necessary for *H. rubra*, could seriously bias estimates of the mortality rate obtained by catch-curve analysis, given that infestation increases with age (Shepherd 1973; Clavier 1992), and the oldest age classes strongly influence the analysis. An advantage of this multiple regression technique is that fewer shells need to be discarded (in this study 20% instead of over 50% which were infested) so the bias in the resultant estimate should be much reduced. The other advantage of the technique is the disclosure of secondary causes of ring deposition, and the determination of the strength of their effect. The disadvantage is that, because these secondary causes of ring deposition as well as the growth rate are likely to vary from place to place, growth studies will need to be carried out at practically every site where shell aging is to be applied. This reduces but does not nullify the usefulness of the technique.

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